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BIOLOGICAL BULLETIN

THE REGULATORY CHANGE OF SHAPE IN PLANARIA DOROTOCEPHALA.

C. M. CHILD.

The recent discovery of *Planaria dorotocephala* Woodworth (Woodworth, '97) in very large numbers, near Chicago, has made it possible for me to use this form for extensive series of experiments. The species is very similar to *P. maculata* in structure, behavior and regulation, but possesses some advantages over that species for experimental work. It attains a larger size, is more active, and can be obtained in unlimited numbers and all ages in this locality, while *P. maculata* is much less abundant. I found the same species in California some years ago (Child, '06), but was unaware at that time that it had been described.

In the present paper only certain experiments concerning the effect of anæsthetics on form regulation will be considered. It is possible by the use of dilute solutions of anæsthetics to control, modify and inhibit various regulatory processes almost at pleasure. For example, head-formation can be made a process of redifferentiation instead of regeneration in almost any desired degree (Figs. 14 and 16) or can be completely inhibited, according to the conditions of the experiments, and the same is true concerning the formation of a new posterior end and a new pharynx, and the regulatory changes in the intestinal branches. Moreover, the use of anæsthetics permits, in greater or less degree, an analysis of some of the various factors concerned, and finally, it is possible by this means to produce individuals capable of continued existence if returned to water which possess characteristics, or perhaps more properly, combinations of characteristics which do not occur in nature.

The anæsthetics chiefly employed in my experiments thus far are

alcohol, ether and acetone-chloroform, commercially known as chloretone. The effects of all are essentially similar in kind, but of course differ quantitatively according to the substance and the concentration. Ether, for example, in a concentration of 0.4–0.5 per cent. produces about the same effect as alcohol in a concentration of 1.5–1.6 per cent. In solutions of these concentrations, individuals and pieces have been kept alive as long as three months, though the resistance differs greatly according to the condition of the animals and various other factors, most of which can be controlled experimentally either directly or indirectly.

In order to avoid as far as possible decrease in concentration of the solution by evaporation the following method has been used. The animals or pieces are placed in Stender dishes of several hundred c.c. capacity with ground edges and a cover with ground groove exactly fitting the edge. The groove is filled with solution of the same concentration as that in the dish so that the dish is sealed so long as the fluid does not evaporate from the groove. After the dishes are thus closed they are placed in larger jars containing a liter or more of the same solution and these are sealed with vaseline and the covers weighted so that no escape of vapor or entrance of air is possible. And finally, all solutions are renewed every forty-eight hours and are made up immediately before using. In this way it is possible to compare the effect of the anæsthetic upon pieces of different size and from different regions of the body and also upon worms in different physiological condition.

This method makes possible the control and modification of form regulation in this species to a greater extent than any other which has been described. At present, however, only certain points will be considered, a full account of the experiments being postponed to a future time.

In several of my "Studies on Regulation" I discussed the changes in shape and proportion which occur in isolated pieces of various species of turbellaria and which, under the usual conditions, constitute an approach to the shape and proportions of the whole animal. These experiments with anæsthetics furnish new data which confirm my earlier conclusions, and it is some of these data which are to be presented here.

I. EXPERIMENTAL DATA.

When whole individuals or pieces are placed in 1.5 per cent. alcohol or in 0.4–0.5 per cent. ether they lose the power of coördinated movement almost entirely for a time. After four to five days, however, they become in some degree acclimated to the new conditions and begin to move about very slowly, but with increasing vigor as time goes on, though they never attain the normal motor activity. Pieces including the old head begin to move about earlier than pieces without a head, for the latter must form a new head before they can regain the usual degree of motor activity, and regulation is greatly delayed in the solution. The important point for the present purpose is that for some days movement, and particularly coördinated locomotion, is almost completely eliminated. It is of interest to determine to what extent regulation occurs under these conditions.

The first experiment to be described concerns pieces including that part of the body anterior to the line *b* in Fig. 1, *i. e.*, short pieces with the old heads. In Fig. 2 a piece of this kind after ten days in 1.5 per cent. alcohol is shown: during this time the piece has moved about but little and that chiefly during the last few days. Fig. 6 represents a similar piece after five days in water, Fig. 7 the same piece after ten days. Comparison of Figs. 2 and 7 shows that regulation in the alcohol is greatly delayed: a little new tissue has been formed at the posterior end, but, as a microscopic examination under pressure shows, it is still a mass of cells without any marked visible differentiation, and it can readily be seen that it is not used as a tail and is not attached to the substratum as the animal creeps slowly about; a small group of cells is present in the pharyngeal region, but these likewise show no marked differentiation. In water, on the other hand, a new tail has been formed which functions in the normal manner, contracting, extending and attaching to the substratum as the animal

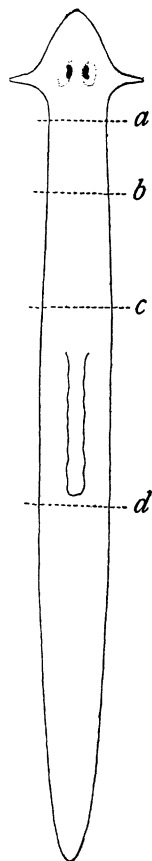
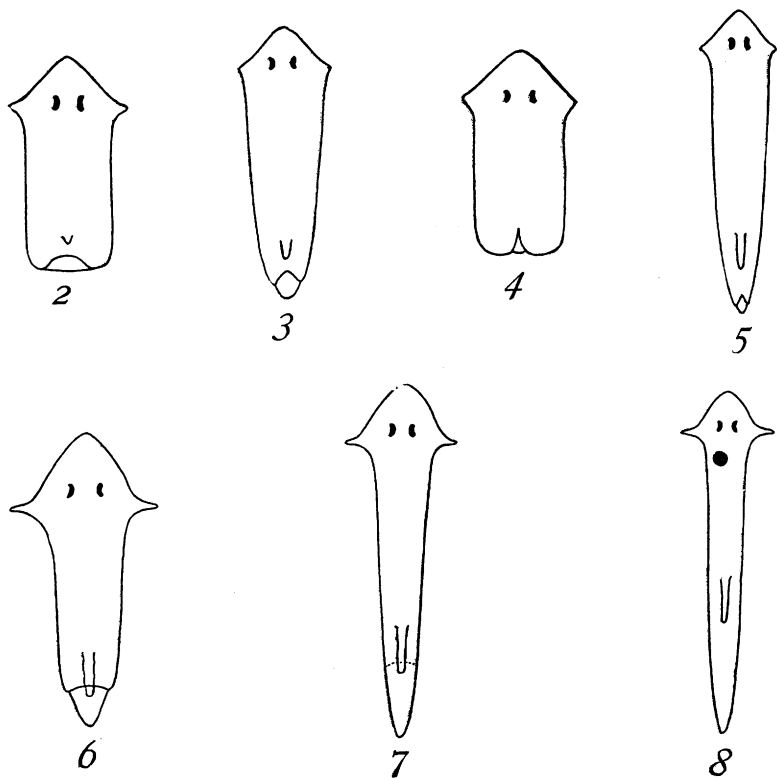


FIG. 1.

creeps; the pharynx is well-developed and sections show that it possesses essentially the same structure as the pharynx in uninjured animals.

But the difference between the two pieces is most marked as regards change of shape. The piece in alcohol has not elongated at all, in fact it has decreased in length and it may be noted incidentally that the "auricles" on the sides of the head are greatly reduced. The piece in water (Fig. 7) has in the same



FIGS. 2-8.

length of time elongated to nearly twice its original length, has become much more slender and tapers posteriorly. This piece has moved about during regulation to an even greater extent than the uninjured animal, for short pieces with the old heads are usually more active than whole individuals.

After ten days the piece in alcohol gradually becomes more

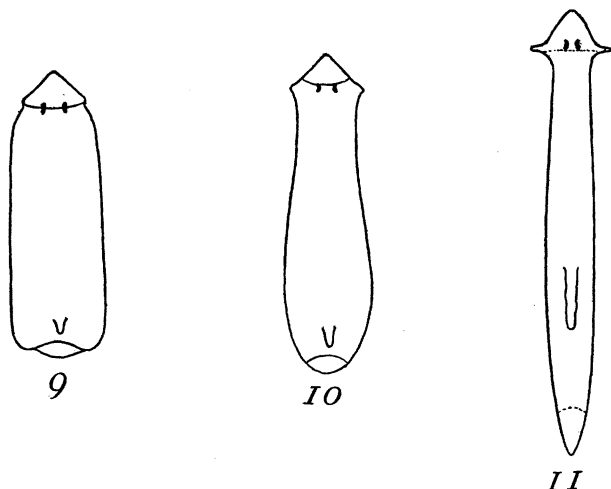
active, though it never attains anything like normal activity. At the end of twenty or twenty-five days it has acquired a shape like Fig. 3. The posterior end now functions as a tail to some extent and attaches itself to the substratum as the animal advances but the amount of new tissue has not increased. The piece may live for six weeks or more in alcohol but it never undergoes any appreciable further change in shape. The newly formed parts undergo some degree of differentiation but never attain the characteristic adult structure. Apparently the piece has attained approximately a condition of equilibrium for the conditions under which it is living.

If the concentration of the solution is gradually increased after the first three or four days it is possible to inhibit practically all regulation beyond the closure of the wound: the pharynx does not appear, no further growth of new tissue at the posterior end occurs, and the piece undergoes no elongation (Fig. 4). Under these conditions the piece does not acquire the ability to move about.

If now these pieces which have attained equilibrium in alcohol be returned to water they gradually resume the process of regulation, but with certain differences from pieces which have not been in alcohol. The chief difference for present purposes is that the outgrowth of new tissue at the posterior end does not proceed until it reaches the usual amount. The tail is formed almost entirely by a redifferentiation of the old tissue (Fig. 5). The pieces may undergo change of shape after their return to water until they attain practically the same shape as pieces which have not been in alcohol. Fig. 5 shows a later stage of Fig. 4 after its return to water and Fig. 8 will serve as regards shape for the late stages of either water or alcohol-water pieces.

These results, which are merely illustrations of what I have observed in several hundred pieces, permit certain conclusions of interest. In the first place it is possible to inhibit entirely the change in shape without inhibiting entirely the processes of redifferentiation and regeneration, and the change in shape can be stopped at any point without stopping entirely other regulatory processes (Fig. 3). On the other hand, if the growth of new tissue from the cut surface is inhibited in earlier stages (Figs. 2

and 4) the change in shape may occur in later stages (especially after return to water) without the formation of more new tissue (Figs. 3 and 5). It follows that the factors determining the change in shape must be in greater or less degree different from those determining the localization and growth of new parts. Moreover, the change in shape occurs only when the piece is capable of locomotion and it is in general proportional to the locomotor ability of the piece.

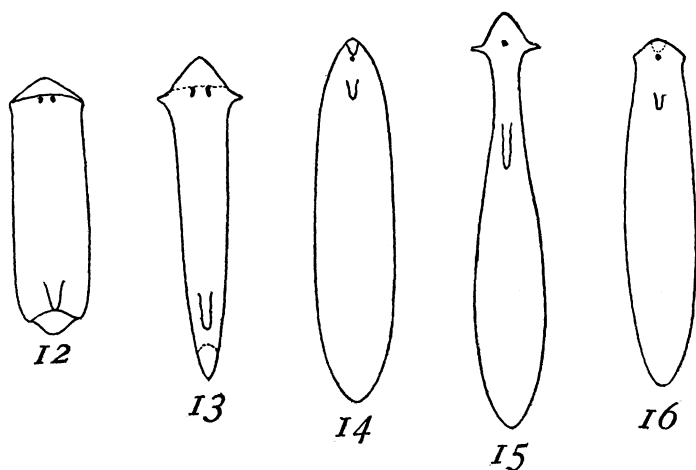


FIGS. 9-11.

But pieces which do not possess the old head afford even more positive evidence for these conclusions. Fig. 9 represents a piece corresponding to the region between the lines *a* and *c* in Fig. 1 after fifteen days in 1.5 per cent. alcohol. A new head has appeared, a small new pharynx is present as a mass of undifferentiated cells, and some new tissue has formed at the posterior end, but the piece as a whole shows no approach to the normal shape: it has undergone no marked changes in proportion. Incidentally it may be noted that the pharynx in such pieces appears much further posteriorly than in similar pieces in water. After seven days more the piece has the shape shown in Fig. 10. It moves about slowly, but its movements are different in character from those of pieces possessing the old head: here the posterior half of the body is very evidently not under complete control,

i. e., is not fully coördinated with the anterior region, and when the animal advances it is simply dragged along as a mass of inert material, its posterior end being only very rarely attached to the substratum. The shape of the piece suggests that the anterior part is being stretched by the strain upon it of the posterior portion, and I believe that is exactly what is occurring.

Similar pieces in water attain in the same length of time the shape and structure shown in Fig. 11. Pieces in alcohol of 1.5 per cent. do not change in shape much beyond the condition shown in Fig. 10, but if they are returned to water they regain their normal locomotor activity and may finally reach a shape like that of Fig. 11.



FIGS. 12-16.

In these cases a new head, a small new pharynx and some new tissue at the posterior end have appeared without any marked change of shape in the piece as a whole (Fig. 9). Evidently the change of shape and the localized formation of new tissue are not necessarily correlated.

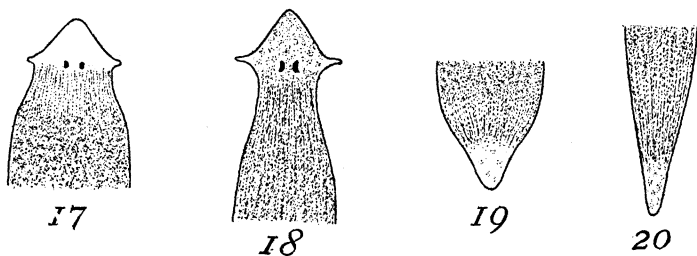
The same thing appears in Fig. 12, which shows a piece from the same region (*a* to *c*, Fig. 1) after fifteen days in 0.5 per cent. ether. Head, pharynx and posterior end have formed but no change in shape has occurred. This piece was returned to water at this stage and after seven days more had attained the shape shown in Fig. 13.

In another series pieces comprising the whole post-pharyngeal region were used (posterior to *d*, Fig. 1). These pieces, after eighteen days in 0.5 per cent. ether, had attained the condition shown in Fig. 14. A small head is forming, almost entirely by redifferentiation, at the anterior end, with one median eye, and a small pharynx is present. At this time half of the pieces were returned to water and half remained in ether. After nine days more the pieces in water had acquired the condition shown in Fig. 15 while those in ether were like Fig. 16. In the pieces returned to water the anterior half is greatly elongated but the posterior half remains much as before. In these pieces, as in the one described above, the posterior part was dragged about by the more active anterior portion. Gradually complete coördination returned and the posterior end began to attach itself to the substratum as the animal advanced and after this the shape gradually approached that of the normal animal.

Further data along this line could be presented but these cases are sufficient to show that it is possible to delay or inhibit the change in shape to any desired degree, and to induce its occurrence at any time. Moreover, the manner in which it occurs can be controlled and altered indirectly by using pieces of different sizes and from different regions of the body.

To my mind the evidence indicates very clearly that the change in shape is primarily a mechanical deformation of the body in consequence of the altered direction of the strains to which it is subjected as the animal advances. To control the change experimentally we have only to control the locomotor activity. In several of my earlier papers (Child, '02, '03, '04a) I have described the method of locomotion in certain species of turbellaria: in *Planaria* longitudinal strain arises in essentially the same manner as in the other forms discussed, the use of the posterior region as an organ of attachment being one of the chief factors. Moreover, there is considerable direct evidence that the tissues of a region undergoing change of shape are being stretched. In regions where the decrease in width and the elongation of the old parts begin, the chromatophores are always greatly elongated, and their elongation is greatest where the change in shape is most rapid. As the change goes on they become drawn out into long

lines. Figs. 17 and 18 indicate this change in shape of the chromatophores in the region posterior to a new head, and Figs. 19 and 20 for a region anterior to a new tail. In the pieces in alcohol and ether this change in shape of the chromatophores appears only when the change in shape occurs, not when the new tissue is formed. In cases where the change of shape is inhibited in the anæsthetic (Figs. 2, 4, 9, 12) it does not appear at all, but if such pieces are returned to water, and the change of shape occurs, the stretching of the chromatophores also appears. In Fig. 14, for example, it did not appear so long as the piece was kept in the ether, but after several days in water it was most conspicuous in the slender anterior region (Fig. 15), this region appearing almost



FIGS. 17-20.

as if finely striped in the longitudinal direction. This change in shape of the chromatophores is actually a stretching, not a migration, for it is possible to select some particular spot which happens to be conspicuous for some reason and to observe its change of shape from day to day: in such cases it can be seen clearly that merely elongation not migration occurs.

A similar elongation is visible in the parenchyme cells in section. Stevens ('07) has recently described this elongation or orientation of the parenchyme cells and regards it as indicating migration, but Steinmann ('08) does not agree with her. As a matter of fact the specimens in which the change of shape is inhibited by anæsthetics show nothing of the sort even in regions adjoining those where new tissue is being formed, but if such pieces be returned to water the cells of the parenchyme become very distinctly elongated or oriented in the direction in which elongation of the body is occurring, even though no new tissue is being formed at the time. In short the change in shape or

arrangement of the parenchyme cells probably has nothing to do with active migration, but merely indicates the direction of the strain which produces deformation.

These histological features then, support and confirm the other observations, and all appear to show that the change in shape is primarily a deformation in consequence of strain rather than a complex physiological process.

There can be no doubt, however, as I have repeatedly pointed out that reactions of various kinds result from the strain and deformation: muscles and other tissues undoubtedly "adapt" themselves to the new relations of parts. In fact there is no apparent reason why the change of shape should not continue indefinitely, or at least until the elasticity of the tissues became involved, if nothing but the mechanical deformation took place. Undoubtedly "functional adaptation" to the altered strains occurs and this determines how far the change shall proceed. Sooner or later the tissues adjust themselves fully to the new conditions, *i. e.*, a condition of equilibrium is attained and change in shape ceases. Under the usual conditions this gives what we commonly call the "normal" shape, but I have shown above that under other conditions the shape may be different. No one would deny, I suppose, that the shape of cells is determined in many cases (*e. g.*, the polyhedral shape of blastomeres in many eggs, the polygonal outline of many epithelial cells, etc.) to a greater or less extent by purely mechanical factors. If this is the case it seems scarcely possible to deny that purely mechanical factors may be concerned in determining the shape and arrangement of parts in animals without hard structures and with tissues of a high degree of physical plasticity. That they are the only factors in such cases, or that because they are factors in some cases, they must be in others, I certainly do not and never have maintained.

In *Planaria* the width of the head is apparently an important factor in determining the width of the body behind it. The head itself is not involved to any appreciable extent in the change of shape. It furnishes, so to speak, a fixed point, or rather region at one end, and between this and the posterior end the change of shape occurs. Consequently, in short pieces, where the new head is small, the change of shape is very much greater than in

long pieces, where it is much broader. In short pieces possessing the old head and consequently capable of rapid and frequent locomotion, the change occurs much more rapidly than in other pieces and the body often becomes much more slender proportionally than that of the "normal" animal and tapers more toward the posterior end. In pieces from the posterior region of the animal the chief region of attachment forms the largest part of the piece. Since attachment occurs by the lateral margins as well as by the tip of this region, the change of shape occurs most rapidly in the regions just behind the new head, for these are the regions where the greatest change in the direction of the strains occurs.

Summing up the data presented, the first point of importance is that no necessary connection exists between the change of shape and the redifferentiation or regeneration of parts: the two processes can be separated from each other almost completely in time, and are often separated in space. Secondly, it is possible to control the change of shape, to inhibit it, to stop it at any point, or to allow it to proceed, by controlling the locomotor activity. And finally, the tissues in regions undergoing change of shape show very distinct indications of physical deformation in the direction of the strains. The conclusion which seems to me to accord most closely with the facts as they now stand is that the change of shape is primarily a mechanical deformation resulting, at least in large part, from the strains which arise in locomotion, these strains being altered in direction and amount in pieces as compared with the whole animal. The final shape, *i. e.*, the cessation of change is probably determined by the physiological reaction of the differentiating or redifferentiating tissues to the altered conditions, and the consequent establishment of an equilibrium.

II. FUNCTION, FORM AND REGULATION.

Since the appearance of my earlier papers on regulation certain reviews and criticisms of the work have appeared. From some of these, particularly from Driesch's review (Driesch, '05) I can only conclude either that I have failed to state my position clearly, or that the reviewers have not become sufficiently acquainted with my work to understand what that position is. Driesch, for example,

has imputed to me certain views which I have not only never held, but which I have expressly repudiated more than once. And recently, in a brief reference to my work, Morgan ('07, pp. 373-4) has cited certain conclusions as mine, which are very different from those which I have reached. I have considered Driesch's criticisms elsewhere (Child, '07) and shall refer to these and other criticisms only incidentally. But a brief statement of my position with regard to certain features of the problems of form and regulation and with especial reference to mechanical factors, movement and use of parts and function in general seems desirable in connection with the new facts presented above.

1. *The Relation between Function and Form.*¹

In a fully developed organ certain processes occur which are concerned with the maintenance of the organism as a whole. These processes may affect either the relations of parts to each other or the relations of the organism as a whole to the external world, or both. They are commonly designated as functions, *i. e.*, the adult organism may be regarded as a complex machine, which works or functions in a characteristic manner.

But the functions characteristic of the adult organs do not appear in development until a certain stage is reached and the organ possesses a certain structure. Apparently then, development up to the stage where function in the above sense begins is a process of machine-building. Roux's distinction between a formative and a functional stage in development expresses this idea.

But how is the machine constructed and what is the agency which constructs it? The material of which the machine is to be made must be acted upon, arranged, transformed, localized, differentiated, etc. Evidently this point of view necessitates the assumption of a special formative agent or agents of some kind. How shall we conceive this formative agent? Pangenesis, determinants, formative substances, entelechies are some of the answers which have been given to this question. All these answers are much alike in that they regard the construction of the organism as a process analogous in some sense to the construction of a

¹ Cf. Child, '06a, p. 402, '07.

machine by human agency. When the machine is constructed it begins to function.

This point of view seems to me to be essentially naive and anthropomorphic : moreover it is responsible for certain "Schein-probleme" which have arisen from time to time, and for certain barren lines of research, particularly in zoölogy, which has been dominated by hypotheses of this general character to a much greater extent than botany.

To my mind life is inconceivable without some sort of function in some sort of structure ; a living structure functions as long as it is alive ; its function is its life. If this view is correct, the organism is functioning in some manner at all stages of its existence, from the earliest to the latest. Function in this sense is physiological activity of all kinds, all transformation and transference of energy.

It is a well established fact that the special functional activity of organs is very generally a factor in their development and differentiation beyond a certain stage, and in the maintenance of their characteristic form and structure after development is completed. In the absence of this functional activity the organ does not develop beyond a certain point and does not persist indefinitely. Functional hypertrophy, atrophy from disuse, functional adaptation, etc., are terms used to designate these relations between function and form.

But the real difference between earlier and later stages of development consists, it seems to me, not in the absence of function at one stage and its presence at another, but rather in the difference in character of function in the different stages. If a particular kind of function determines the structure and differentiation at one stage, and we know that it does this, is there not a logical basis for the belief that the functions which exist in other stages are also formative factors in those stages ?

In other words, is there not good reason to believe that every stage of development is directly or indirectly the necessary consequence of the functional activity in the preceding stage ? According to this view each stage of development is a machine in the broad sense and each is the product of the activity of a pre-existing machine. External factors play a part, particularly in

plants and in the simpler animals, in determining the character of the machine and its activity, but this fact does not essentially alter the case.

Viewed from this standpoint, development, from its earliest stages on, is just as strictly a functional process as functional differentiation or functional hypertrophy in the stricter sense. This view does not necessitate the assumption of any special formative factors* different in character from functional processes as the factors behind or underlying development. The formative factors of each stage are the functional activities of the immediately preceding stage (plus external factors). The process of development of the organism is not essentially different from the process of maintenance after development. Indeed strictly speaking, development ceases only when death occurs. The germ cell is an organism possessing a certain structure and function, and this forms the starting point. The functional activity in this structure determines the next stage of development, *i. e.*, a change in structure and therefore a change in function. This process continues and at the same time gradually approaches a condition of physiological equilibrium.

This view of development is of course no more an "explanation" than is the assumption of an entelechy or that of determinants. As a point of view, however, and as a basis for attacking the problem of morphogenesis it possesses a certain value in that it does away with various assumptions and places the problem of morphogenesis on a strictly physiological basis. To say that all organic form and structure are functional in their origin is merely to say that the problem of morphogenesis is a physiological problem and nothing more.

This is the position which I have held since the beginning of my work on regulation. I have used the word "function" with reference to any and all physiological processes and activities at any and all stages of development and have repeatedly called attention to this fact.¹

¹ It is somewhat surprising, therefore, to find Driesch ('05, p. 790; '07, p. 180) pointing out that I have put the cart before the horse in regarding function as a determining factor in form regulation, since, as he says, an organ develops "for function" and does not function until it is developed, or at least until a certain stage of development has been reached. The difference between Driesch and myself on this

When we come to consider the process of development somewhat more in detail we find that two complex groups of internal factors must be considered, viz., constitution and correlation. This, of course, is true of any machine: its function depends upon the constitution and correlations of its parts, provided, of course, that the necessary external conditions for function are present. In different organisms and in different features of development the two factors may of course play a very different part.

2. *Functional Regulation and Form Regulation.*

It follows from what has been said that all form regulation is, according to my definition, either directly or indirectly functional regulation, *i. e.*, the physiological processes in the structure involved determine what the result of regulation shall be (Child, '06c).

In certain cases among the turbellaria I have been able to control, inhibit and modify the process of form regulation to a greater or less extent by controlling and modifying, in most cases indirectly, the movement and use of the parts most intimately involved in the regulatory processes (Child, '02, '03, '04a-c, '05a-d). This work showed very clearly that movement and use of parts were important factors in certain cases and certain features of regulation: they may even be primary factors in determining certain results. It is just as certain, however, that in many other cases they play no part at all.¹

point is in reality merely one of definition; he limits the term "function" to the processes of which I spoke in the first paragraphs of this section, while I regard all processes in the organism as functions. His criticism of my position is of course entirely beside the point since he substitutes his definition for mine. Physiological processes of some kind certainly occur even in the earliest stages of development, and that these are functions of an existing structure cannot be doubted. I believe that they are also the formative factors in development.

Morgan ('07) calls attention to the fact that the functional idea is not new. This of course is true; it is the position which every physiologist must hold in one form or another. I have never considered that I was formulating a new hypothesis of development; I have merely attempted to apply certain physiological ideas to the phenomena of form regulation. Among botanists this view has been very generally held for a long time.

¹ Morgan ('07, p. 374) apparently believes that I regard movement as a universal factor in form regulation, for he calls attention to the fact that movement does not occur in many cases of regeneration. But I have repeatedly asserted that my conclusions upon the effect of movement concerned only certain species and certain features of regulation (Child, '02, p. 218, p. 229; '04a, p. 131; '04b, p. 467, etc.).

As I pointed out concerning *Leptoplana* (Child, '04a) movement is undoubtedly not a factor of importance in determining the formation of new tissue at a cut surface, but experimental evidence indicates clearly enough that it is a factor in determining the rapidity, amount and direction of growth and to a greater or less extent the character of its differentiation.

In the experiments on *Planaria* described above, the head and pharynx, for example, do not attain their "normal" shape and structure when movement is largely inhibited by anæsthetics. By the use of the higher concentrations it is possible to inhibit in almost any desired degree the process of form regulation so far as visible morphogenesis is concerned. Pieces which in water form heads very rapidly may be prevented entirely from forming heads by the proper use of the anæsthetic, or almost any intermediate condition between these two extremes may be attained by the formation of incomplete or partial heads. Pieces incapable of forming heads in the anæsthetic, regain their original power when returned to water. But it does not in the least follow from these facts that head formation is entirely the result of actual movement. My position is, and has been, that movement is merely one of the functional activities concerned in development, and which usually concerns later stages to a greater extent than earlier. But in regeneration in the turbellaria and in various, though by no means all, other forms a peculiar condition exists in that new tissue adjoins fully developed parts which may be in active movement. There can be no doubt that movement of these adjoining old parts influences conditions in the new tissue and so affects the result, either quantitatively or qualitatively or both. But movement and functional activity in the stricter sense, in which Driesch uses the word, are certainly far from being universal factors in either form regulation or ontogeny.

Whatever the importance of movement in a particular case, it is merely one of a great variety of functional factors. In many cases movement and motor use of parts are not concerned at all in regulation and in some other cases it is evident that while movement may affect the later stages this movement is possibly only in consequence of preceding regulation. In *Cestoplana* (Child, '05b), for example, where the posterior portion of an an-

terior piece becomes visibly "posterior" as regards the character of its movements before any marked structural changes occur, regulation must have occurred before such changes in movement could appear.¹

3. *Mechanical Regulation and Morphallaxis.*²

In the first of the "Studies" the idea of mechanical regulation as the chief factor in the change of shape in pieces of *Stenostoma* was developed. According to my conception mechanical regulation is primarily a mechanical deformation of physically plastic tissues. Whether we consider regulation as a return or approach to the normal condition after a disturbance of this condition (Driesch, '01), or as a return or approach to a condition of physiological equilibrium after a preceding condition of equilibrium has been disturbed (my own definition), mechanical regulation in my sense

¹ In my paper I referred to these changes as functional regulation and called attention to the altered character of the movement as indicating that they had occurred, but while the movement is undoubtedly a factor in what follows, it would be absurd to suppose that it is the primary factor in such a case.

² Some years ago, in describing the course of regulation in *Planaria maculata*, Morgan called attention to the peculiar changes in shape which the pieces undergo, these changes consisting mainly in a decrease in width and an increase in length. Concerning this process he says: "Thus the relative proportions of the planarian are attained by a remodelling of the old tissue. I would suggest that this process of transformation be called a process of morphallaxis" (Morgan, '98, p. 385). Later ('00) he applied the same term to the changes in shape and proportion in *Hydra* and other forms. So far as I am aware, Morgan has not stated at any time whether the term "morphallaxis" is to be applied to the whole process of form regulation in *Planaria* and other forms, including the regeneration and redifferentiation which occurs, or only to the changes in shape and proportions of the piece. From the quotation given above it would appear that he intended it to apply only to the change in shape and proportions, but in his latest statement ('07, p. 15) he apparently applies the term to the whole process of form regulation by redifferentiation. In my earlier "Studies" I used the term with reference only to the changes in proportion and shape: later, however, I substituted "change in proportions" for it as less ambiguous for my purposes (Child, '05a, p. 253). Driesch ('01) considered the term as synonymous with "Restitution durch Umdifferenzierung," a very different meaning from that which I had given it in my work. It is probable that Driesch's misunderstanding of my conclusions concerning form regulation is in part due to our different interpretations of this term.

In several of my earlier papers the word "form" was used for "shape" and "outline." I agree with Driesch that this use of the word may be misleading, but I was careful to distinguish between form in this sense and structure, and pointed out that the factors concerned with change in form probably had nothing to do in many cases with change in structure (Child, '02, p. 218).

is theoretically possible, provided certain characteristic mechanical conditions exist in the normal animal and are altered in characteristic manner in the piece. In several of the "Studies" the changes in shape in pieces of *Stenostoma*, *Leptoplana* and *Cestoplana* were shown to be apparently primarily mechanical regulations (Child, '02, '04a, '05a, '05c) and it was suggested that similar processes might occur elsewhere. The recognition of mechanical regulation is not in any sense an attempt to interpret regulation in general on a mechanical basis (cf. Child, '02, p. 229): it concerns merely changes in shape and outline. Mechanical regulations are possible only under the conditions mentioned above, and whether they occur or not can only be determined by investigation of each particular case. It is not necessary to suppose that all cases of "morphallaxis" (in the sense of change in shape and proportions) are mechanical regulations. If they are they certainly depend on different mechanical conditions in different cases. In *Hydra*, for example, the factors determining the change in shape are certainly not the same as in *Planaria*, and may not be mechanical at all. In the cases which I have considered mechanical strains arise in connection with locomotion and these strains are altered in a characteristic manner in isolated pieces and, as I have shown, the changes in shape are exactly what might be expected in physically plastic material under these conditions. Mechanical regulation is to be expected only in organisms or parts possessing a considerable degree of physical plasticity and where skeletal structures are not concerned. As regards the shape of animals in general gross mechanical factors are certainly unimportant as compared with others, or not concerned at all, and I have never even suggested that such factors were of general significance (cf. Driesch, '05, p. 790). On the other hand, it seems to me absurd to deny that characteristic strains or pressures existing in plastic material may play some part in determining shape.

That the changes in shape in pieces of *Stenostoma*, *Leptoplana*, *Cestoplana*, and *Planaria* are not primarily "functional adaptations" (cf. Driesch, '05, p. 766) is, I think, evident. A functional adaptation, as I understand it, is a change in structure which involves a change in functional capacity, either an increase

or a decrease or a modification in kind according to the character of the factor inducing the change. The change in shape in the pieces of *Planaria*, etc., does not in itself involve any such change in functional capacity, moreover, functional adaptations to mechanical tension and pressure consist, usually if not always, in an altered resistance to the mechanical factor, not in a change of shape which accords with the laws of mechanics. The change in shape in these turbellaria is essentially similar to what would occur under the same conditions in any material of similar physical constitution and there is not the slightest evidence that it results from a change in functional capacity.

There is little doubt, however, that functional adaptations result from the change of shape: as was suggested above, it is probable that the cessation of the change and the final attainment of a more or less characteristic shape, *i. e.*, a condition of equilibrium, is in part the consequence of the functional reaction of the differentiating and redifferentiating tissues to the altered mechanical conditions. In other words, the change of shape brings about the functional adaptation instead of resulting from it.

But even though these changes in shape do not appear to be functional adaptations in Driesch's sense, they are functional regulations in my sense, and probably the simplest possible kind of functional regulation.

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